PROC. ENTOMOL. SOC. WASH.
91(2), 1989, pp. 133–142

THE UNIQUE PURRING SONG OF *CHRYSOPERLA COMANCHE* (BANKS), A GREEN LACEWING OF THE *RUFILABRIS* SPECIES GROUP (NEUROPTERA: CHRYSOPIDAE)

CHARLES S. HENRY

Professor of Biology, Department of Ecology and Evolutionary Biology, Box U-43, 75 North Eagleville Road, The University of Connecticut, Storrs, Connecticut 06268.

Abstract.—The courtship song of *Chrysoperla comanche*, a common green lacewing from western North America, is described and compared to that of its apparent closest relative, *C. rufilabris*. It was found to consist of a single long (about 15 seconds) volley of abdominal vibration, producing a substrate-borne signal that steadily increased in amplitude from beginning to end. Its primary frequency averaged about 87 Hz at 27°C, and was modulated in amplitude by simultaneous low frequency vibrations caused by slower oscillations of the abdomen. Both sexes made identical calls, and each female answered the male's signal halfway through his song. Temperature affected the song's phenotype, so linear regression equations were used to compare features at any temperature. Unique song characteristics shared between *C. comanche* and its sister species, *C. rufilabris*, reflect their close relationship and phylogenetic distinctness from the *Chrysoperla carnea* group.

Key Words: Chrysopidae, *Chrysoperla*, courtship, acoustical, communication

The green lacewing taxon *Chrysoperla* Steinmann has recently been accorded full generic status (Séméria 1977), yet further subdivision may be necessary to represent the evolutionary divergence that has occurred within its boundaries. Currently, the genus is defined by morphology, bionomics, and behavior: its members share a common ground plan of male genitalia and wing venation, feed as adults principally on honeydews rather than plant lice, overwinter as diapausing adults, and must "sing" to one another before mating (Séméria 1977, Hagen and Tassan 1966, Sheldon and MacLeod 1974, Henry and Johnson in press). However, more careful scrutiny of genitalia in particular indicates that at least two natural species groups of *Chrysoperla* can be recognized (Agnew et al. 1981, Adams pers. commun.). The better studied of these, the *carnea* group (Tauber and Tauber, 1987), includes the common North American species *C. plorabunda* (Fitch), *C. downesi* (Banks), and *C. mohave* (Banks). The other group, known as the *rufilabris* group, is characterized by male genitalia that are unique among *Chrysoperla*; its members are most easily recognized by their relatively narrow, apically pointed hind wings, and by the bright red stripe usually present on the facial area (genae) of the head. *Chrysoperla rufilabris* (Burmeister), *C. harrisii* (Fitch), *C. externa* (Hagen), and *C. comanche* (Banks) belong to this lineage.

Singing during courtship and mating is a characteristic of all *Chrysoperla* species, and has been studied in both of the species groups. These songs are actually bouts or volleys of male or female abdominal quivering/jerking that vibrate leaves, twigs, or conifer needles with substrate-borne, low frequency signals (Henry 1979)—a phenomenon known as tremulation. The signals display complex frequency and amplitude modulation and are highly consistent and unique within each species. Both sexes sing, reciprocally exchanging their signals in prolonged duets, and in most species, the two sexes produce identical songs (Henry 1980a, b, c, 1985a). Within the recognized and undescribed species of the *carnea* group in North America and Europe, the songs have been shown to have a species-isolating effect, preventing hybridization between otherwise interfertile cryptic species (Henry 1985a, b, 1986).

The *rufilabris* group of *Chrysoperla* may also use vibrational calls in this way, but only the common *C. rufilabris* has been analyzed in any detail (Henry 1980a). Here, I describe the peculiar tremulating songs of the sister species of *C. rufilabris, C. comanche*, from two sites in California. This species was originally described from Texas and is found throughout southwestern North America (Bickley and MacLeod 1956, Agnew et al. 1981). It is a common resident of orchards and vineyards at low elevation and occurs sympatrically with *C. rufilabris* at many localities. Just as *C. rufilabris* has song features not found in the *carnea* group, the call of *C. comanche* is of most unusual design and dynamics, reflecting and reinforcing the distinct phylogenetic position of the *Chrysoperla rufilabris* lineage.

METHODS AND MATERIALS

I collected adults of *Chrysoperla comanche* at two sites in California, 220 km apart, during late September, 1987. Twelve were obtained in the early afternoon of 24 September, 1987, from the southern tip of Sequoia National Forest, two kilometers south of Isabella Lake, Kern County, at an elevation of about 1000 meters. The collecting area was very dry and hot (34°C), with scattered 5–10 meter-tall scrub oak (*Quercus dumosa* Nuttall) and larger (to 20 meters) digger pine (*Pinus sabiniana* Douglas). All were flushed from the oaks by prodding the branches with an insect net. Twenty-one other adults were obtained from a citrus grove just northeast of the town of Mentone, San Bernardino County, at about 500 meters elevation. These were collected at dusk (26°C) by beating the branches of 8 meter-tall lemon trees. Phillip Adams (California State University, Fullerton) chose this second site and assisted in procuring and identifying the insects there. All were mailed to my laboratory in Connecticut. The specimens from each population were maintained as a separate breeding colony, referred to as Isabella or Mentone. Adults were supplied with a water and Wheast™ diet (Hagen and Tassan 1966, Henry 1983b). Eggs were removed daily and larvae reared on ether-killed *Drosophila* spp., as described in Henry (various papers). Photoperiods of 17:7 daylight : darkness and temperatures of 25 ± 1°C resulted in rapid growth and continual reproduction in the laboratory. Several field-collected individuals were tested for reproductive and singing behavior, but the majority of tests were performed on first and second laboratory generations. The songs of six males and seven females from Isabella Lake and three males and one female from Mentone were analyzed in detail. Of these, one male and two females from Isabella Lake and one male and one female from Mentone were original, field-caught individuals.

Adult males showed courtship activity within 24 hours of eclosion, and females after three days. Therefore, tests were initiated on week-old individuals, and continued for about one month (lifespan averaged 140 days). During testing, each lacewing was placed individually or with a partner in a small cardboard coffee cup covered with plastic wrap. Vibrations from abdominal jerking were monitored from the plastic surface with a piezoelectric transducer connected to a Tektronix® digital oscilloscope, amplifier/speaker, and cassette tape recorder, as described in earlier papers (Henry 1985a, b).

For analysis, recorded signals were digitized by a Cambridge Electronics Design CED1401 12-bit A/D,D/A device and transferred to an IBM PC-AT microcomputer. Multiple-slice fast-Fourier transforms (FFT's) and accurate measures of elapsed time could then be performed on the signals with the WATERFALL® software package of Cambridge Electronics Design, Ltd. Frequency and time data were keyed into the spreadsheet, Microsoft EXCEL®, for further analysis and reduction, and could then be transferred (through ASCII and DIF file conversion) to programs like Asyst Software Technologies' ASYSTANT+® for statistical analysis or Jandel's SIGMAPLOT® and Advanced Graphics Software's SLIDEWRITE for graphing.

A lacewing song (= call) is a vibrational entity that an individual produces once or at irregular intervals. Each may consist of one, or many, volleys (= bouts) of abdominal vibration, and those volleys are organized into "shortest repeated units" (SRU's), composed of at least one but often several volleys delivered with some consistent temporal spacing. During a duet, each participant repeatedly answers its partner with the SRU characteristic of the species. In *C. comanche*, the song is best described as a single volley, so the terms song, call, volley, bout, and SRU are synonyms.

Because the features of lacewing songs vary with temperature, data were collected at 20 to 28°C to calculate linear regression equations. Results could then be normalized to a standard temperature, 27°C, to compare means and standard deviations among different subsets of data or between taxa. I measured eight major features (Tables 1, 2, 3, and Fig. 1) of the songs of *C. comanche*, using 71 male and 89 female volleys at 8 different temperatures. These features were specifically chosen to facilitate comparison with *Chrysoperla rufilabris* (Table 3; Figs. 1, 2, 5; Henry 1980a). To compare the slopes of the temperature regressions of different song features or different populations or taxa, Q_{10} (the factor by which a feature changes over a 10°C rise in temperature) was determined for each song component. This factor is obtained by calculating the expected value of the feature at 20 and 30°C from the linear regression and dividing the larger value by the smaller (Table 4).

Significant differences were recognized where the means of two normally distributed samples differed from one another by a two-tailed t-test using confidence limits of 99% or better. These are marked in the tables with triple asterisks (***). Values following a ± sign are one standard deviation of the mean.

Voucher specimens were deposited in the entomological collection of the University of Connecticut. Some were frozen at −90°C for future protein and DNA analysis.

RESULTS

Mating in *C. comanche*, as in other lacewings of the genus *Chrysoperla*, was preceded by a long, well-defined courtship in which the partners exchanged volleys of abdominal vibration. These songs, usually produced spontaneously and identically by both males and females under a wide range of temperature and light conditions, occurred most often at 25°C or above and during the last hour of daylight. Individuals also sang in response to the call of another insect, or to a recorded or synthesized song of the correct structure and duration played through a small (12 cm) loudspeaker. The shortest repeated unit (SRU) of the song consisted of a single prolonged volley of abdominal vibration, lasting about 15 seconds at 27°C (Fig. 1; Tables 1, 2, 3). The song, when heard through headphones, resembled a long, drawn out "purr" that began at the threshold of audibility and slowly built to a crescendo, then diminished quickly at its conclusion with one or two secondary bursts of vibration. The fundamental or pri-

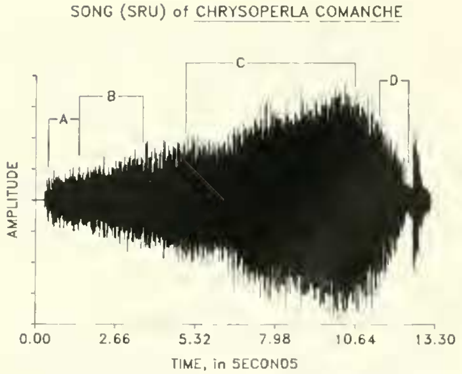

Fig. 1. Digitized oscillograph of the shortest repeated unit (SRU or volley) of the call of *Chrysoperla comanche*, showing principal parameters A–D defined in text and referenced in tables. A, initial volley frequencies; B, early middle volley frequencies; C, late middle volley frequencies; D, end-of-volley frequencies.

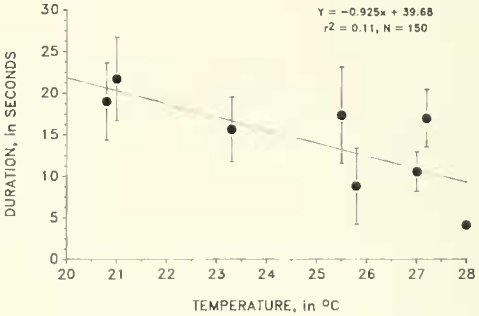

Fig. 3. Effect of temperature on volley duration for all calls of all males and females of *Chrysoperla comanche*. The filled circle at each temperature is the mean of at least 15 volleys delivered at that temperature, and the error bars bracket one standard deviation of the mean. The linear regression equation, its squared variance, and its sample base are entered above the line plot.

mary frequency of vibration averaged 86–88 Hz during the major, central portion (B and C of Fig. 1) of each volley. Each call started (A) and ended (D) at slightly but significantly lower frequencies of about 75 and 79 Hz, respectively (Table 3). In addition, the primary frequency was modulated by a lower frequency, high amplitude oscillation whose frequency similarly increased, leveled off, and then decreased during the course of each volley. The mean of this modulation frequency was about 21 Hz, but started at approximately 14 Hz and stopped at 17.5 Hz (Table 3). It was clear from watching receptive lacewings at low temperatures that this modulating oscillation corresponded to gross vertical movements of the insect's abdomen, while the higher, primary frequency was produced by a low-amplitude abdominal "buzzing" superimposed on the low-frequency carrier (Fig. 2). At high temperatures, primary and modulating frequencies were both high enough and of sufficiently low amplitude to render the motions of the abdomen nearly invisible.

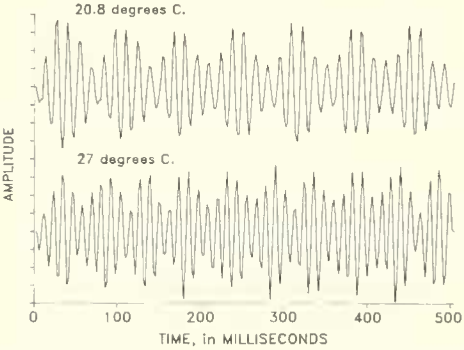

Fig. 2. Digitized oscillographs of half-second fragments of songs produced at two different temperatures by a solo female *Chrysoperla comanche*. Spikes within a volley are strokes of the individual's abdomen and constitute the primary frequency of the call. The regular variations in overall amplitude are caused by the modulating frequency.

Males and females sang identically, in every respect (Tables 1, 2, 3). In 27 of 36 observed heterosexual duets, the female answered a spontaneous call produced by the male well before the male completed his song. When the female finished, a few seconds passed before the male initiated another volley, and then the female again began to sing partway through the male's song. Thus *C. comanche* duets were not "polite," in the sense of nonoverlapping. In fact, the beats that were produced from the acoustical interaction between two su-

Table 1. Principal characteristics of the songs of individual males of *Chrysoperla comanche*, normalized to 27°C. Means and standard deviations are tabulated, with the number of measured volleys entered parenthetically. Averages and standard deviations of the means are shown in the bottom rows. The letters A to D refer to the parts of the song specified in Figure 1.

	Males							
	Abdominal Vibration Frequency (strokes/second)				Modulation Frequency (maxima/second)			Song Duration (seconds)
Indiv.	Initial (A)	Mid1 (B)	Mid2 (C)	End (D)	Initial (A)	Mid (C)	End (D)	
1	—	91.63	90.82	88.14	12.84	22.79	20.76	18.16
	—	± 1.35	± 1.37	± 2.20	—	± 0.43	± 1.47	± 5.65
	—	(7)	(7)	(7)	(1)	(7)	(5)	(7)
2	—	90.38	87.15	85.01	15.34	22.72	21.20	21.60
	—	± 1.13	± 0.05	± 0.50	—	± 0.45	± 0.00	± 4.19
	—	(4)	(4)	(4)	(1)	(4)	(4)	(4)
3	77.72	88.11	86.88	81.86	12.87	19.70	16.09	11.15
	± 4.16	± 2.41	± 3.00	± 3.11	± 1.64	± 1.02	± 1.44	± 4.17
	(4)	(8)	(9)	(9)	(4)	(8)	(6)	(9)
4	77.56	86.64	85.55	81.10	8.35	20.85	17.09	17.99
	± 3.13	± 2.33	± 1.21	± 2.69	—	± 0.75	± 1.77	± 3.58
	(12)	(16)	(16)	(11)	(1)	(16)	(2)	(15)
5	70.16	89.56	87.48	81.03	—	21.74	18.56	18.01
	—	± 0.73	± 0.47	± 4.32	—	± 0.37	± 1.61	± 5.43
	(1)	(6)	(6)	(4)	—	(6)	(3)	(4)
6	72.17	90.86	87.79	77.01	—	20.54	—	16.29
	± 5.91	± 2.19	± 1.52	± 5.91	—	± 0.94	—	± 6.00
	(4)	(5)	(5)	(4)	—	(5)	—	(5)
7	75.92	86.18	83.98	80.47	16.20	21.93	20.13	17.14
	± 0.00	± 3.40	± 1.78	± 0.76	± 4.24	± 0.39	± 3.02	± 10.52
	(2)	(7)	(7)	(7)	(5)	(7)	(6)	(7)
8	68.28	85.17	84.99	72.51	14.51	20.13	16.11	13.56
	± 5.12	± 1.08	± 1.24	± 2.01	± 2.36	± 0.68	± 1.53	± 3.29
	(11)	(11)	(11)	(11)	(5)	(11)	(11)	(11)
9	73.92	89.71	85.63	81.09	—	22.25	18.33	18.06
	± 2.45	± 2.28	± 0.33	± 3.20	—	± 0.43	± 1.42	± 4.84
	(5)	(6)	(6)	(6)	—	(6)	(6)	(6)
Avg:	73.68	88.69	86.70	80.91	13.35	21.41	18.53	16.88
SD:	3.66	2.27	1.99	4.42	2.79	1.14	2.02	3.00
N:	7.00	9.00	9.00	9.00	6.00	9.00	8.00	9.00

perimposed tones of similar but not identical frequency were very audible over headphones during the overlapping phases of the songs. One to ten of such sequences always occurred before copulation. Just prior to copulation, the distinctions between male and female calls became unclear: in five observed copulations, each partner sang without pause during the final 15 seconds of courtship, producing a cacophony of substrate-borne noise. The last phase of courtship was also characterized by a five to ten second period of wing bumping and mutual abdominal tapping, as in *C. rufilabris* and most other lacewing species.

Insects were tested and measured at a number of different temperatures. Data for three of the eight principal song features are graphed against temperature in Figs. 3 and 4, with the linear regression equations placed

Table 2. Principal characteristics of the songs of individual females of *Chrysoperla comanche*, normalized to 27°C. Means and standard deviations are tabulated, with the number of measured volleys entered parenthetically. Averages and standard deviations of the means are shown in the bottom rows. The letters A to D refer to the parts of the song specified in Figure 1.

	Females							
	Abdominal Vibration Frequency (strokes/second)				Modulation Frequency (maxima/second)			Song Duration (seconds)
Indiv.	Initial (A)	Mid1 (B)	Mid2 (C)	End (D)	Initial (A)	Mid (C)	End (D)	
1	—	89.40	88.50	85.75	—	22.03	—	17.01
	—	± 1.96	± 1.13	± 1.40	—	± 0.58	—	± 6.15
	—	(3)	(3)	(2)	—	(3)	—	(3)
2	78.59	86.90	85.69	82.04	13.14	21.49	16.64	7.69
	± 2.80	± 1.56	± 0.95	± 3.37	± 2.72	± 0.33	± 2.27	± 4.60
	(5)	(6)	(6)	(6)	(3)	(6)	(6)	(6)
3	79.72	88.17	86.75	83.29	13.34	20.75	19.12	13.56
	± 3.46	± 1.60	± 1.02	± 2.96	± 3.54	± 1.34	± 2.10	± 2.67
	(4)	(9)	(9)	(6)	(2)	(9)	(4)	(9)
4	76.49	86.50	84.89	76.10	14.23	21.25	16.01	11.91
	± 2.94	± 1.14	± 0.89	± 3.33	± 2.87	± 0.35	± 1.63	± 3.85
	(16)	(22)	(22)	(22)	(6)	(22)	(22)	(20)
5	72.58	86.85	85.31	78.46	15.34	21.27	18.36	16.48
	± 4.31	± 1.69	± 1.14	± 3.35	± 1.28	± 0.48	± 1.45	± 3.27
	(9)	(18)	(18)	(18)	(3)	(18)	(17)	(17)
6	73.66	88.68	84.90	79.53	—	21.41	17.09	12.07
	—	± 1.75	± 1.60	± 1.91	—	± 0.41	± 0.42	± 6.05
	(1)	(4)	(4)	(4)	—	(4)	(4)	(4)
7	70.61	90.09	88.19	79.31	—	19.76	16.75	16.39
	± 4.10	± 2.25	± 1.33	± 2.51	—	± 0.32	± 1.11	± 2.67
	(5)	(10)	(10)	(9)	—	(10)	(9)	(10)
8	81.00	87.42	84.52	78.10	12.56	21.56	17.33	11.39
	± 1.65	± 2.66	± 1.36	± 1.99	± 1.81	± 0.74	± 1.16	± 6.62
	(10)	(17)	(17)	(15)	(5)	(15)	(12)	(14)
Avg:	76.09	88.00	86.09	80.32	13.72	21.19	17.33	13.31
SD:	3.91	1.31	1.55	3.14	1.09	0.68	1.07	3.21
N:	7.00	8.00	8.00	8.00	5.00	8.00	7.00	8.00

beside each graph. Volley/SRU duration (Fig. 3) varied inversely with temperature, but the correlation was not very good: the regression coefficient, R^2, was a low 0.11. All primary and modulating frequency components (Fig. 4) showed a direct, linear temperature relationship, and those in the middle portions of the call were tightly correlated with temperature changes ($R^2 = 0.84$ to 0.85). The Q_{10} values calculated from the regression equations (Table 4) were statistically equivalent for all frequency components of the calls. Compared with *C. plorabunda* and *Chrysopiella minora* Banks, however, pitch alterations of the songs of *C. comanche* were less pronounced for a given temperature change.

The temperature regression equations allowed conversion of all measured values to their equivalents at 27°C. Individual lacewings varied little in their normalized average values for most of the principal song features (Tables 1 and 2). When different populations of insects were compared (Table 3), males were insignificantly different from females, and Isabella Lake individuals

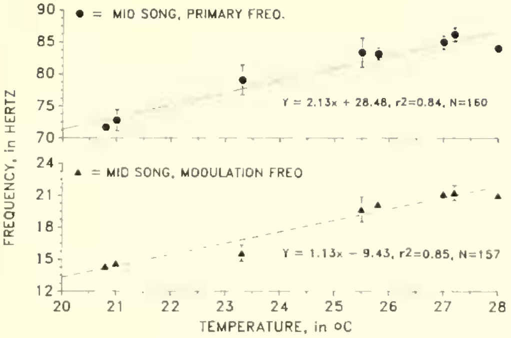

Fig. 4. Effect of temperature on the primary and modulation frequencies of the mid-volley portion of the songs of all males and females of *C. comanche.* The filled circle or triangle at each temperature is the mean of at least 15 volleys delivered at that temperature, and the error bars bracket one standard deviation of the mean. The linear regression equation, its squared variance, and its sample base are entered below each line plot.

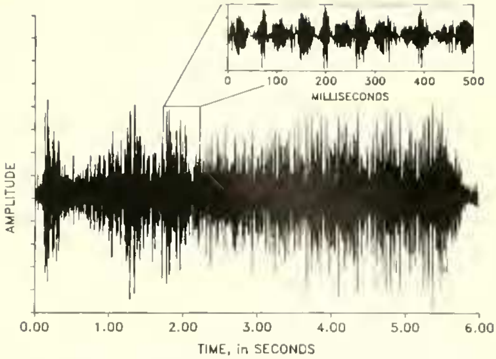

Fig. 5. Digitized oscillograph of the shortest repeated unit (SRU or volley) of the male "long call" of *Chrysoperla rufilabris.* Inset is a half-second section taken from the middle of the volley, which shows eleven individual oscillations of the abdomen (black smears). Note the absence of a clear frequency structure; the abdomen strikes the substrate and generates high-frequency noise.

were essentially identical to those from Mentone. Only one call feature showed significant differences between compared samples: Mid2 primary frequency in the Isabella and Mentone populations differed by 2 Hz. Song duration was the most variable of the measured song parameters among individuals (Tables 1 and 2).

Discussion

The song of *Chrysoperla comanche* was found to be unique among those that have been described for eleven other species of its genus. First, it is characterized by the longest unbroken volley of any North American lacewing, averaging nearly 15 seconds in duration, but occasionally exceeding 30 to 35 seconds. The species that most nearly matches *C. comanche* in volley length is its North American sister species, *C. rufilabris,* with volleys of four to eight seconds (Henry 1980a). Another species with volleys of comparable length is the undescribed P3 sibling of *C. plorabunda.* Its volleys, produced several per SRU, can be as long as eight seconds in individuals from the Kofa Mountains of Arizona (unpublished data). The only lacewing species that seems to exceed *C. comanche* in volley length is an undescribed relative of *C. carnea* from near Ticino in the southern Alps of Europe. A volley in this species may last for more than two minutes. However, this case may not be strictly comparable, because each long bout of abdominal vibration in the Ticino form actually consists of numerous, independent short volleys repeated about eight times per second (Henry 1983a).

A second remarkable feature of the *C. comanche* call is the modulation of the primary abdominal vibration frequency by regular, intense oscillations of lower frequency. Some green lacewings that produce a series of short volleys in rapid succession approach but do not attain the condition seen in *C. comanche.* For example, a sibling species of *C. downesi* from the redwood forests of California (Founder's Grove) repeats its short volleys at nearly 10 per second (unpublished data), and two sibling species of *C. carnea* from different parts of the Alps of Switzerland may attain volley repetition rates of about eight per second (Henry 1983a,

Table 3. Principal characteristics of the songs of *Chrysoperla comanche*, normalized to 27°C and averaged for all measured volleys produced by males versus females (upper section of table) or produced by individuals from Isabella Lake versus Mentone, California (lower section). The corresponding features of the songs of *Chrysoperla rufilabris* are entered at the bottom of the table for comparison. Mean values and standard deviations are tabulated, with the number of measured individuals (column 1) or volleys (all other columns) entered parenthetically. Significant differences (between rows) at the 1% level are indicated by asterisks. N/a = not applicable.

	Abdominal Vibration Frequency (strokes/second)				Modulation Frequency (maxima/second)			Song Duration (seconds)
	Initial (A)	Mid1 (B)	Mid2 (C)	End (D)	Initial (A)	Mid (C)	End (D)	
All Males: (N = 9)	73.66 ± 5.50 (39)	88.06 ± 2.94 (70)	86.41 ± 2.35 (71)	80.40 ± 5.24 (63)	14.21 ± 3.23 (17)	21.19 ± 1.21 (70)	18.21 ± 2.56 (43)	16.36 ± 5.76 (67)
All Females: (N = 8)	76.51 ± 4.57 (50)	87.54 ± 2.14 (89)	85.64 ± 1.67 (89)	78.70 ± 3.68 (82)	13.70 ± 2.39 (19)	21.14 ± 0.82 (87)	17.13 ± 1.76 (74)	13.36 ± 4.97 (83)
All Isabella: (N = 13)	75.67 ± 4.38 (61)	88.06 ± 2.38 (118)	86.42 *** ± 2.04 (119)	80.19 ± 4.48 (106)	13.59 ± 2.50 (21)	20.45 ± 1.22 (118)	16.47 ± 2.37 (82)	14.90 ± 5.03 (112)
All Mentone: (N = 4)	74.37 ± 6.57 (28)	86.94 ± 2.78 (41)	84.71 *** ± 1.37 (41)	77.41 ± 3.87 (39)	14.42 ± 3.17 (15)	20.95 ± 0.96 (39)	16.99 ± 2.17 (35)	14.13 ± 6.83 (38)
Totals: (N = 17)	75.26 ± 5.17 (89)	87.77 ± 2.53 (159)	85.98 ± 2.03 (160)	79.44 ± 4.49 (145)	13.94 ± 2.79 (36)	21.16 ± 1.01 (157)	17.53 ± 2.14 (117)	14.70 ± 5.53 (150)
Chrysoperla rufilabris: (N = 10, 28 C)	n/a	n/a	n/a	n/a	— — —	18.20 ± 1.11 (116)	— — —	5.15 ± 1.23 (183)

1985a). In contrast, *C. comanche*'s signals consist of long, continuous volleys, with no pauses in primary abdominal vibration activity between the amplitude peaks (Fig. 2). Also, the rate or frequency of modulation, about 21 Hz, is higher by a factor of two or more than in species with discrete, rapidly repeated volleys. The interaction of the primary and modulation frequencies at two temperature extremes is illustrated in Fig. 2.

The universal pattern of singing within the *carnea* group of *Chrysoperla* is the production of identical SRU's alternately by each individual of a courting pair. Whether these are single volleys or complex series of volleys, those of one partner do not overlap or acoustically interfere with those of the other. In contrast, duets in *C. comanche* are not "polite"; the female typically answers the male halfway through his one-volley call, and then both partners often sing simultaneously for several minutes before copulating. Similarly, in *C. comanche*'s closest North American relative, *C. rufilabris*, the male produces a song consisting of a single, long volley of abdominal vibration, and the receptive female also answers the male in the middle of his volley (Henry 1980a).

Other basic song features are shared between *C. comanche* and *C. rufilabris* (compare Figs. 1 and 5). In both species, the SRU is an exceptionally long volley of abdominal vibration that increases steadily in amplitude to a crescendo near its end. Neither species seems to repeat its long volleys at any regular interval: the volley, SRU, and song are all one and the same. And finally, both species modulate the intensity of their calls with very low frequency, high amplitude oscillations of the abdomen, at ap-

Table 4. Q_{10} factors over the range of 20 to 30°C for each of the principal features of the songs of all individuals of *Chrysoperla comanche*. Corresponding values for *Chrysoperla plorabunda* (Henry 1983b) and for *Chrysopiella minora* (Henry and Johnson in press) are also tabulated. N/a = not applicable.

Species	Abdominal Vibration Frequency (strokes/second)				Modulation Frequency (maxima/second)			Song Duration (seconds)
	Initial (A)	Mid1 (B)	Mid2 (C)	End (D)	Initial (A)	Mid (C)	End (D)	
Chrysoperla comanche (N = 17)	1.19	1.32	1.30	1.28	1.18	1.86	1.67	1.78
Chrysoperla plorabunda (N = 10)	1.61	1.47	1.47	1.25	n/a	n/a	n/a	1.83
Chrysopiella minora (N = 15)	1.80	1.81	1.81	1.71	n/a	n/a	n/a	2.77

proximately the same rate: 21 Hz in *C. comanche*, and 17 Hz in *C. rufilabris*. These shared characteristics probably reflect the close phylogenetic relationship between the two species, because such traits are not found in the *carnea* group of *Chrysoperla*.

However, important differences also exist between *C. comanche* and *C. rufilabris*. First, *C. rufilabris* has sexually dimorphic calls, which were not found in *C. comanche*. Male *C. rufilabris* usually produce long volleys, but females answer with much shorter bursts of abdominal vibration and have not been found to produce anything resembling the male SRU (Fig. 5; see also fig. 1F and G in Henry 1980a). Second, the song of *C. rufilabris* is devoid of any primary frequency structure analogous to that of *C. comanche*; only lower frequency oscillations, corresponding to *C. comanche*'s modulation frequency, are apparent (Fig. 5, inset). It is possible that *C. rufilabris*, unlike other lacewings that tremulate, strikes the substrate with its abdomen, because considerable 500 Hz noise is carried on the 17 Hz amplitude peaks (Fig. 5, inset). Whatever the cause, the songs of the two species are distinctive and "sound" different from one another through headphones, despite their several shared characteristics.

Whether or not *C. comanche* and *C. rufilabris* can interbreed is unknown. The two species overlap geographically, thus providing the potential for hybridization: *C. rufilabris* occurs commonly in fields and meadows throughout most of North and Central America, including the American Southwest and California (Bram and Bickley 1963), and *C. comanche* has been collected at many sites in California, Arizona, New Mexico and Texas (Bickley and MacLeod 1956). Both species reproduce continually under long daylight conditions, suggesting prolonged overlap in their breeding seasons in areas of sympatry. Although the relevant breeding experiments remain to be done, the pronounced differences between the songs of the two sister species probably preclude successful interspecific courtship and mating.

The phylogenetic position of another common member of the *rufilabris* group, *C. harrisii*, is uncertain. It, too, sings during courtship, but its song is a peculiar, prolonged session of untidy, almost random vibrational bursts, and has not yet been characterized in detail. Its dark green color, conifer-associated habits, and unique male genitalia (Bram and Bickley 1963) make it easy to distinguish from *C. rufilabris* or *C. comanche*, and its song has not been found to exhibit any of the features shared by *C. rufilabris* and *C. comanche*. This indicates that the latter two species are more closely related to each other than either is to *C. harrisii*, and that *C. harrisii* may be the sister group of the *rufilabris-comanche* lineage. The reproductive behavior of the fourth relative of these species, *C. externa*, has not been investigated.

My studies of *C. comanche* and its relatives suggest that singing behavior has taken a different evolutionary direction in the *rufilabris* group of *Chrysoperla* than it has in the *carnea* group. It also provides evidence for separating *Chrysoperla* into two genera, to avoid the confusion of species groups. In both groups, singing is essential to courtship, and is complex in most species, perhaps because of the reinforcement of behavioral isolating "mechanisms" in genetically similar, potentially interbreeding taxa (Butlin 1987). However, polite duets between partners have developed principally in the *carnea* group, while the three members of the *rufilabris* group have acquired long, overlapping calls that may involve drumming on the substrate rather than tremulation.

ACKNOWLEDGMENTS

This work was supported by National Science Foundation award BSR-8508080, Charles S. Henry Principal Investigator. I thank my research assistant and wife, Julie J. Henry, for help in maintaining living lacewings. Phillip Adams (California State University, Fullerton) helped greatly in the collection and identification of specimens, but, more importantly, provided me with the conceptual background in chrysopid taxonomy and phylogeny that made this study possible. Special thanks go to an anonymous reviewer, who worked hard to improve the clarity of the manuscript.

LITERATURE CITED

Agnew, C. W., W. L. Sterling, and D. A. Dean. 1981. Notes on the Chrysopidae and Hemerobiidae of eastern Texas with keys for their identification. Southwestern Entomol., suppl. 4: 1–20.

Bickley, W. E. and E. G. MacLeod. 1956. A synopsis of the nearctic Chrysopidae with a key to the genera (Neuroptera). Proc. Entomol. Soc. Wash. 58: 177–202.

Bram, R. A. and W. E. Bickley. 1963. The green lacewings of the genus *Chrysopa* in Maryland (Neuroptera: Chrysopidae). Univ. Maryland Agric. Exp. Stn., Bull. A-124: 1–18.

Butlin, R. K. 1987. Species, speciation, and reinforcement. Am. Nat. 130: 461–464.

Hagen, K. S. and R. L. Tassan. 1966. The influence of protein hydrolysates of yeast and chemically defined diet upon the fecundity of *Chrysopa carnea* Steph. Vest. csl. Spol. Zool. 30: 219–227.

Henry, C. S. 1979. Acoustical communication during courtship and mating in the green lacewing *Chrysopa carnea* (Neuroptera: Chrysopidae). Ann. Entomol. Soc. Am. 72: 68–79.

———. 1980a. Acoustical communication in *Chrysopa rufilabris* (Neuroptera: Chrysopidae), a green lacewing with two distinct calls. Proc. Entomol. Soc. Wash. 82: 1–8.

———. 1980b. The courtship call of *Chrysopa downesi* Banks (Neuroptera: Chrysopidae): Its evolutionary significance. Psyche 86: 291–297.

———. 1980c. The importance of low-frequency, substrate-borne sounds in lacewing communication (Neuroptera: Chrysopidae). Ann. Entomol. Soc. Am. 73: 617–621.

———. 1983a. Acoustic recognition of sibling species within the holarctic lacewing *Chrysoperla carnea* (Neuroptera: Chrysopidae). Syst. Entomol. 8: 293–301.

———. 1983b. Temperature-induced changes in the calls of the green lacewing, *Chrysoperla plorabunda* (Neuroptera: Chrysopidae). Psyche 90: 343–360.

———. 1985a. Sibling species, call differences, and speciation in green lacewings (Neuroptera: Chrysopidae: *Chrysoperla*). Evolution 39: 965–984.

———. 1985b. The proliferation of cryptic species in *Chrysoperla* green lacewings through song divergence. Fla. Entomol. 68: 18–38.

———. 1986. Good vibrations. Natural History 95: 46–53.

Henry, C. S. and J. B. Johnson. In Press. Sexual singing in a non-chrysoperlan green lacewing, *Chrysopiella minora* Banks. Can. J. Zool.

Séméria, Y. 1977. Discussion de la validité taxonomique du sous-genre *Chrysoperla* Steinmann (Planipennia, Chrysopidae). Nouv. Rev. Entomol. 7: 235–238.

Sheldon, J. K. and E. G. MacLeod. 1974. Studies on the biology of the Chrysopidae. 5. The developmental and reproductive maturation rates of *Chrysopa carnea* (Neuroptera, Chrysopidae). Entomol. News 85: 159–169.

Tauber, C. A. and M. J. Tauber. 1987. Inheritance of seasonal cycles in *Chrysoperla* (Insecta: Neuroptera). Genet. Res., Camb. 49: 215–223.